SECTION 11 THEORETICAL BIOLOGY

Section Leader J.A.J. Metz

GENERAL INTRODUCTION

The section organises its activities around the grand unifying theory of biology: Darwinism. Biological entities, or organisms, are distinct from those of physics and chemistry by the fact that they reproduce. That they do so only almost faithfully is the main cause of their present day diversity and complexity. Moreover, they are composed from parts, presently even more so than in the early days, leading to a combinatorial explosion of possibilities: the space of possible organism is nearly empty. To understand its population, it is necessary to integrate studies of the principles by which organisms are built (development), their inner workings (function and so-called internal selection), the workings of the selective arena (population and community ecology), and the history of their descent (phylogeny). The section provides a single home for the IBL theoreticians active in these various arenas, thus creating a platform for the cross-fertilisation of disciplines, as well as of techniques, be they statistical, computational, or mathematical. Moreover, their independent affiliation allows the members of the section a great diversity of collaboration with the empirically oriented sections of the IBL, or outside the IBL if theoretical developments so demand. Historically, the section concentrated mainly on the phenotypic level, a strategy justified by the weak and contorted link between the genotypic and the phenotypic levels, and the apparent domination of the selective regime in determining many features of great biological interest, as corroborated by the predictive power of the theory. The theories of physiologically structured populations and of adaptive dynamics can be counted as internationally recognised successes. In more recent years the interface towards the genetic level is attracting more attention, with i.a. activities in the area of evo-devo, and RNA function.

Research Projects:

1. ***Bio-Informatics and Self-Organising Systems***

This project aims to contribute to the field of Bio-informatics by data-mining and the simulation of complex systems, and to the theory of self-organising complex systems. In the theme there is a distinct stress on intracellular processes, in particular those relating to the secondary and tertiary structure of RNA in relation to its function and evolution.

2. *Innovations and Constraints in Evolution*

This project focuses on innovations and mechanisms that facilitate evolutionary changes at the organismal level, in particular the constraining effects of internal selection, i.e., selection caused by characteristics of the developmental system. The main focus is on the conservation of the early organogenesis stage and on the conservation of adult traits that are determined during that stage, with the goal of understanding the interplay between genetic architecture, developmental mechanisms and stabilising selection.

3. *Ecological Dynamics and ESS Theory*

This project considers the population dynamics of single species as well as processes involving the interaction between several species on ecological time scales. In one direction novel mathematical tools are developed for the translation from complex individual level causes to population dynamical consequences. In the opposite direction the ESS route allows the prediction, based on their population dynamical consequences, of properties of individuals. In addition statistical methods are developed for analysing ecological data as well as data on individuals, in a manner useful for evolutionary theorising.

4. *Adaptive Dynamics*

This project considers evolutionary time-scales and the species level as well as between-species interaction. The aim here is the construction of an overarching theory of phenotypic evolution, as a direct dynamical extension of the evolutionary statics of ESS theory. This theory also deals with co-evolution and with the treelike structure of character evolution through adaptive speciation

5 *Methodological Foundations of Phylogenetics*

This project aims to contribute to the development of conceptual and methodological issues in, as well as data analytical and computational techniques for, Phylogenetic Systematics.

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Project 1. ***Bio-Informatics and Self-Organising Systems***
(Dr. A.P. Gultyaev, Dr. F.H.D. van Batenburg)

A potential for the formation of inhibitory structures in ribozymes has been analysed. Comparison of the potential hairpins possible in natural ribozymes and sequences selected *in vitro* shows that natural evolution tends to eliminate stable helices incompatible with the functional fold, whereas RNAs evolved *in vitro* are less optimised in this respect (“frustrated”). This evolutionary trend is determined by kinetic effects in RNA folding, and is presumably less pronounced in artificial RNAs due to a restricted evolutionary history. This suggests that many artificial ribozymes can be further improved using a strategy to eliminate or destabilise base-pairs conflicting with the functional structures. (Sacha Gultyaev)

Evolutionarily conserved functional structures have been predicted for the gene enod40 mRNAs from a number of leguminous plants. The conserved structural motifs, in particular, specific internal loops in stem-loop structures, probably play a role in the activity of enod40 during the formation of plant root nodules. (Sacha Gultyaev, in collaboration with the group of Prof. Dr. H.P. Spaink, IBL)

A detailed secondary structure model has been established for the 5’proximal regions of the RNAs from the arterivirus group. It was shown that the specific RNA hairpin, involved in the regulation of arterivirus RNA transcription, is also conserved in coronaviruses. (Sacha Gultyaev, in collaboration with the group of Dr. E. Snijder, LUMC)

Project 2. ***Innovations and Constraints in Evolution***
(Dr. F. Galis, Prof. Dr. J.A.J. Metz, Dr. T. van Dooren)

Although the main focus of the project is on the conservation of adult traits of vertebrates that are determined during the early organogenesis stage (in particular the number of cervical vertebrae in mammals and the number of digits in tetrapods) the extended and segmented germband stage (or phylotypic stage) in insects has been studied in order to obtain a better understanding of the general importance of the factors involved in evolutionary conservation. (Frietson Galis, Hans

Metz, Tom van Dooren)

Considerable progress has been made in determining the importance of deleterious pleiotropic effects in shaping the pattern of evolutionary change (or its absence). We have concentrated on deleterious effects associated with changes in the number of cervical vertebrae in humans. 500 spontaneously aborted and still-born human fetuses were investigated. The incidence of changes in the number of cervical vertebrae and their association with congenital abnormalities in these fetuses has been determined. These results have been compared with those on thoracic and lumbar vertebrae. The prediction that the frequency of changes in the number of cervical vertebrae in early mortality would be significantly higher than in the general population has been confirmed, indicating internal selection against these changes. The prediction that the internal selection would be due to an association of changes in the number of cervical vertebrae with other abnormalities has also been confirmed. Finally, we predicted considerably weaker or even no selection against changes in the number of thoracic or lumbar vertebrae. It was indeed found that the frequency of the latter changes (with the exclusion of those cases that also have changes in the number of cervical vertebrae) was not higher in spontaneously aborted and stillborn fetuses than in the general population. Furthermore, the apparent absence of selection corresponded, as expected, with a lack association between congenital abnormalities and changes in the number of thoracic and lumbar vertebrae. (Frietson Galis and Tom Van Dooren, in collaboration with Dr. Liliane Wijnaendts (pathologist), VUMC, Dr. Hans Feuth (internal diseases) and Dr. F.M. Helmerhorst (gynaecologist), LUMC)

Project 3. ***Ecological Dynamics and ESS Theory***
(Dr. P. Haccou, Prof. Dr. J.A.J.Metz)

A manuscript of a book on branching processes in biology, to appear with Cambridge University Press, has been completed. (Patsy Haccou, in collaboration with Prof. Peter Jagers, Gothenburg, and Prof. Vladimir Vatutin, Moscow)

Optimal management strategies were derived to prevent a population from becoming extinct in a fluctuating environment, when the population size before the risky period is not directly observed, based on dynamic programming with incomplete state observation. To this end the method used previously was generalised to a multiple year situation. (Patsy Haccou, in collaboration with Dr. Hiroyuki Yokomizo and Prof. Yoh Iwasa, Fukuoka)

A method was derived to calculate the expected long-term viability of populations where deleterious mutations have multiplicative fitness effects. The result has been used to compare the effect of different reproductive modes: several forms of thelytoky, arrhenotoky, paternal genome elimination. This way it was found that haplo-diploidy (males somatically haploid) gives a much higher viability than diploidy, and that recombination is disadvantageous in this case. Several forms of thelytoky give a much higher viability than clonal reproduction, and for some forms higher recombination rates increase viability. (Patsy Haccou, in collaboration with Vicky Schneijder, Animal Ecology)

Odd though this may seem, almost the whole of population genetics is based on the Hardy-Weinberg assumption. Yet, this assumption only holds when there is no difference whatsoever in the life history parameters of the sexes, a situation almost never realised in nature. As part of a program to extend the mathematical technology for physiologically structured populations, some approximation formulas have been developed for the calculation of invasion fitnesses for new alleles in genetically polymorphic populations with the potential for a different demography of the sexes. (Hans Metz)

Project 4. ***Adaptive Dynamics***

(Prof. Dr. J.A.J. Metz, Dr. P. Haccou, Dr. T. Van Dooren, drs. J. Beltman, drs. M. Durinx, drs. C. Rüffler)

It has been shown that the so-called canonical equation of adaptive dynamics, so far derived only for unstructured population models, is also applicable for the most general physiologically structured populations at point equilibria. Only a few coefficients change. This extension has become possible thanks to the recent work on integral equation formulations of structured population models, undertaken together with Prof. Mats Gyllenberg (Turku) and Prof Odo Diekmann (Utrecht) in the context of project 3, and a number of branching process results made accessible in the book on branching processes mentioned under that project. A manuscript on this topic is included as section 7.8 in that book. The more technical parts of the proof will de part of a large manuscript on adaptive dynamics for physiologically structured populations, to be finished in spring 2004, that will form the main part of the thesis of Michel Durinx. (Hans Metz and Michel Durinx)

It has been shown that the local normal form for the invasion fitness function near to a singular point in a higher dimensional trait space, that was derived in the previous period for the simplest possible population dynamics of the Lotka-Volterra and simple resource competition type, actually holds good for any physiologically structured population at point equilibrium. During the derivation a large number of technical mathematical points that were left over from the simpler cases were resolved. These results and the surrounding technicalities will form the main part of the manuscript mentioned in the previous paragraph. (Michel Durinx and Hans Metz)

Using the canonical equation of adaptive dynamics as a tool, the biological conditions were determined under which the development of sexual dimorphism prevails over adaptive speciation, and vice versa. The model shows analytic links between saddle points in traits that are allowed to differ in a male-female system, and branching points in clonal models. The implication is that what is often automatically perceived to be a situation that leads to (the initiation of) speciation, based on clonal models, may depending on the circumstances, actually lead to different male and female morphs. (Tom Van Dooren and Michel Durinx)

The technique of Fitness Landscape Plots, developed earlier was employed in a new role to analyse cases of polymorphic evolution. These plots are an extension of Levins' fitness sets to density and frequency dependent selection scenarios. A manuscript on the classification of Evolutionarily Singular Points by means of these plots was completed, which i.a. meant including these latest results, and accepted. (Claus Rüffler, Tom Van Dooren, and Hans Metz)

An adaptive dynamics style extension of a model by Wilson and Turelli (1986) for the evolution of specialisation was developed. These authors investigated the scope of protected polymorphism of a consumer in the presence of two discrete resources by means of a one-locus two allele model. The adaptive dynamics model allows the investigation of the evolutionary dynamics over a continuous trait space. (Claus Rüffler) In another attack on the specialisation problem it was shown that neither a trade-off in general nor a strong trade-off in particular is sufficient for the evolution of specialization. (Claus Rüffler, in collaboration with Martijn Egas, UvA) Manuscripts on each topic are expected to be finished early in 2004.

Learning about environmental features may play a role in speciation, because it sometimes influences both mating behaviour and the location where young are produced. This may lead to speciation in three steps: (i) colonization of a new habitat, (ii) genetic divergence of the two groups by adaptation to the habitats, and (iii) a decrease of genetic mixing between the lineages. A gene-culture coevolutionary model has been used to examine under what circumstances such "speciation by the learning of habitat features" can take place. First the effect has been modelled that the learning of habitat features has on mate choice and on the location where young are produced as two separate parameters. It has been shown that when these effects are stronger, genetic divergence becomes either easier or more difficult, depending on other circumstances (published in January 2004; Joost Beltman, Patsy Haccou and Carel ten Cate). Next, an adaptive dynamics approach has been employed to examine the selection pressures on the strength with which learning influences mate choice and the location where young are produced, both before and after genetic divergence. It has been shown that, as soon as two genetically different lineages have evolved, the decrease of genetic mixing is straightforward: there is then selection toward producing young more frequently in the habitat that individuals exploit themselves, and toward stronger assortative mating between individuals that use the same habitat. When genetic divergence between the groups fails, speciation still often occurs because selection favours producing young in the own habitat. As a result, genetic divergence may succeed at a later evolutionary stage, after which a decrease of genetic mixing completes speciation as before. (Joost Beltman and Patsy Haccou, in collaboration with Carel ten Cate, Behavioural Biology) The resulting manuscript has been submitted.

Next, an adaptive dynamics approach was used to consider the evolution of both an ecological trait, and two traits that determine respectively the genetic and learned component of the habitat preference. It has been shown that when the learned component of habitat preference becomes more important, disruptive selection on the ecological trait occurs in a larger area of the parameter space. Therefore, learning can be said to promote speciation (because disruptive selection is a prerequisite for speciation). However, it has also been found that learned habitat preference is unlikely to evolve before disruptive selection is present, because selection on the genetic component of habitat preference is stronger. Finally, it has been examined what happens as soon as there is disruptive selection: does it indeed lead to speciation, and does this occur via a learned or via a genetic habitat preference? Results from an individual-based version of the model show that, when loci are completely unlinked, and learning confers only little cost, the presence of disruptive selection on the ecological trait is most likely to lead to speciation via the simultaneous evolution of a learned habitat preference. For high costs of learning, speciation is more likely to occur through the simultaneous evolution of a genetic habitat preference, but only when the number of loci coding for the traits is small. For larger numbers of loci, recombination prevents completion of speciation: when the (physical) linkage between loci is increased, speciation through a genetically determined habitat preference more readily occurs. (Joost Beltman and Patsy Haccou, in collaboration with Carel ten Cate, Behavioural Biology) The resulting manuscript will be submitted in 2004.

An edited book on Adaptive Speciation, to appear with Cambridge University Press has been completed. (Hans Metz, in collaboration with Ulf Dieckmann, IIASA, Michael Doebeli, UBC, and Diethard Tautz, Cologne)

Project 4 ***Methodological Foundations of Phylogenetics***

(Dr. M. Zandee, Prof. Dr. D. Kornet)

All methods used in historical biogeographic analysis aim to obtain resolved area cladograms that represent historical relationships among areas in which monophyletic groups of taxa are distributed. When neither widespread nor sympatric taxa are present in the distribution of a monophyletic group, all methods obtain the same resolved area cladogram that conforms to a simple vicariance scenario. In most cases, however, the distribution of monophyletic groups of taxa is not that simple. A priori and a posteriori methods of historical biogeography differ in the way in which they deal with widespread and sympatric taxa. A posteriori methods are empirically superior to a priori methods, as they provide a more parsimonious accounting of the input data, do not eliminate or modify input data, and do not suffer from internal inconsistencies in implementation. It was found that when factual errors are corrected, the exemplars presented in recent literature that purport to show inconsistencies in implementation by a posteriori methods actually corroborate the opposite. The rationale for preferring a priori methods thus corresponds to ontological rather than to epistemological considerations. Two different research programs were identified, cladistic biogeography (associated with a priori methods) and phylogenetic biogeography (associated with a posteriori methods). The aim of cladistic biogeography is to fit all elements of all taxon-area cladograms to a single set of area relationships, maintaining historical singularity of areas. The aim of phylogenetic biogeography is to document, most parsimoniously, the geographic context of speciation events. The analysis of recent contributions made clear that cladistic biogeography using a priori methods is an inductivist/verificationist research program, whereas phylogenetic biogeography is hypothetico-deductivist/falsificationist. The conclusion is that cladistic biogeography can become hypothetic-deductive by using a posteriori methods of analysis. (Rino Zandee)

PERSONNEL

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Dr. N. (Nelly) van der Hoeven	Guest Researcher
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ALW	Netherlands Foundation for Life Sciences
EU	European Union
UL	Leiden University

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- University of Beireuth, Germany, Drs Marc Steigenga

GRANTS

- EU: Postdoc (T. van Dooren) as part of a programme together with IIASA, Turku, Bergen and Paris for research on "Modern Life-History Theory and Its Application to the Management of Natural Resources") from September 2000 for three years. Euro 36,300 plus Euro 5,000/year.
- NWO-ALW: AIO (J. Beltman) "Sexual imprinting, song learning and gene-culture coevolution: modeling the evolution of brood parasitism in birds", August 2000 for four years + Euro 1,362 reiskosten + Euro 226 materiaalkosten
- NWO-ALW: AIO (M. Durinx) "Developing a bifurcation theory for Evolutionary Stable Strategies", from 1 September 2000 for four years. + Eur 709 reiskosten.
- NWO-ALW: AIO (C. Rueffler) "Putting life history theory in a realistic ecological context" from 1 September 2000 for four years + Eur 709 reiskosten.

PUBLICATIONS

Beltman, J.B., **P. Haccou**, C. ten Cate. The impact of song learning on the evolution of interspecific brood parasitism. Behavioural Ecology 14 (2003): 917-923.

Cadet, C., R. Ferrière, **J.A.J. Metz** and M. van Baalen. The Evolution of Dispersal under Demographic Stochasticity. The American Naturalist 162 (2003): 427-441.

Diekmann, O., M. Gyllenberg and **J.A.J. Metz.** Steady State Analysis of Structured Population Models. Theoretical Population Biology 63 (2003): 309-338.

Doebeli, M. and **U. Dieckmann** (2003). Speciation along environmental gradients. Nature 421: 259–264.

Engelhard, G.H., **U. Dieckmann** and O.R. Godø (2003). Age at maturation predicted from routine scale measurements in Norwegian spring-spawning herring (*Clupea harengus*) using discriminant and neural network analyses. ICES Journal of Marine Science 60: 304–313.

Galis, F. and **J.A.J. Metz**. Anti-cancer selection as a source of developmental and evolutionary constraints. Bioessays 25 (2003): 1035-1039.

Galis, F. and B. Sinervo. Conserved early embryonic stages. In: Hall, Brian K. and Wendy M. Olson (Eds) (2003). Keywords and Concepts in Evolutionary Developmental Biology. Harvard University Press, Cambridge M.A.

Galis, F., M. Kundrát and B. Sinervo. An old controversy solved: Bird embryos have five fingers. Trends Ecol. Evol. 18 (1) (2003): 7-9.

Galis, F., G.P. Wagner and E.L. Jockusch. Why is limb regeneration possible in amphibians but not in reptiles, birds and mammals? Evolution & Development 5:2 (2003): 208-220.

Galis, F. Book Review of: Gerd B. Müller and Stuart A. Newman

(Eds) (2003). Origination of Organismal Form. Beyond the Gene in Developmental and Evolutionary Biology Meaning. Acta Biotheoretica 51 (2003): 237-238.

Gårdmark, A., **U. Dieckmann** and P. Lundberg (2003). Life-history evolution in harvested populations: The role of natural predation. Evolutionary Ecology Research 5: 239–257.

Girard, G. A. Roussis, **A.P. Gultyaev**, C.W.A. Pleij and H.P. Spaink. Structural Motifs in the RNA Encoded by the Early Nodulation Gene *enod40* of Soybean. Nucleic Acids Research 31 (2003): 5003-5015.

Grift, R.E., A.D. Rijnsdorp, S. Barot, M. Heino and **U. Dieckmann** (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology Progress Series 257: 247–257.

Gyllenberg, M., **F.J.A. Jacobs** and **J.A.J. Metz**. On the concept of attractor for community-dynamical processes II: The case of structured populations. Journal of Mathematical Biology 47 (2003): 235-248.

Haccou, P. and V. Vatutin. Establishment success and extinction risk in autocorrelated environments. Theoretical Population Biology 64 (2003) 303-314:

Haccou, P., O. Glaizot and C. Cannings. Patch leaving strategies and superparasitism: an asymmetric generalized war of attrition. Journal of Theoretical Biology 225 (2003): 77-89.

Heino, M. and **U. Dieckmann** (2003). Reaction norms for age and size at maturation in Atlantic cod stocks. ICES-GLOBEC Newsletter 10: 3–4.

Hemerik, L. and **N. van der Hoeven**. Egg distributions of solitary parasitoids revisited. Entomologia Experimentalis et Applicata, 107 (2003): 81-86.

HilleRisLambers, R. and **U. Dieckmann** (2003). Competition and predation in simple food webs: Intermediately strong trade-offs maximize coexistence. Proceedings of the Royal Society London Series

B 270: 2591–2598.

Jacobs, F.J.A. and **J.A.J. Metz**. On the concept of attractor for community-dynamical processes I: The case of unstructured populations. Journal of Mathematical Biology 47 (2003): 222-234.

Law, R., D.J. Murrell and **U. Dieckmann** (2003). Population growth in space and time: Spatial logistic equations. Ecology 84: 252–262

Le Galliard, J., R. Ferrière and **U. Dieckmann** (2003). The adaptive dynamics of altruism in spatially heterogeneous populations. Evolution 57: 1–17.

Magori, K., B. Oborny, **U. Dieckmann** and G. Meszéna (2003). Cooperation and competition in heterogeneous environments: The evolution of resource sharing in clonal plants. Evolutionary Ecology Research 5: 787–817.

Parvinen, K., **U. Dieckmann**, M. Gyllenberg and **J.A.J. Metz**. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. Journal of Evolutionary Biology 16 (2003): 143-153.

Reydon, T.A.C. Discussion: Species Are Individuals – Or Are They? Philosophy of Science 70 (2003): 49-56.

Reydon, T.A.C. Philosophy of science in seven easy lessons (Book Review of Philosophy of Science: A Very Short Introduction by Samir Okasha). Metascience 12 (2003): 235-237.

Reydon, T.A.C. (2003). Book review of The Nature of Diversity: An Evolutionary Voyage of Discovery by Daniel R. Brooks and Deborah A. McLennan. History and Philosophy of the Life Sciences 25: 133-135.

Reydon, T.A.C. (2003). Book review of Darwin and Design: Does Evolution Have A Purpose? by Michael Ruse. Human Nature Review 3: 480-483.

Reydon, T.A.C. (2003). Book review of Genes, Categories, and Species: The Evolutionary and Cognitive Causes of the Species Problem by Jody Hey. Quarterly Review of Biology 78: 357.

Reydon, T.A.C. Boekbespreking van Darwins Moordbekentenis: De Ontwikkeling van het Denken van Charles Darwin door Johan Braeckman. Algemeen Nederlands Tijdschrift voor Wijsbegeerte 95 (2003): 73-74.

Schipper, M. and **E. Meelis**. Making Sequential Analysis of Environmental Monitoring Data Feasible by Simplifying the Covariance Matrix Structure. Journal of Agricultural, Biological and Environmental Statistics 8 (2003): 122-137.

Shudo, E., **P. Haccou** and Y. Iwasa. Optimal choice between feedforward and feedback control in gene expression to cope with unpredictable danger. Journal of Theoretical Biology 223 (2003): 149-160.

Stronkhorst, J., C. Schipper, J. Brils, M. Dubbeldam, J. Postma and **N. van der Hoeven**. Using marine bioassays to classify the toxicity of Dutch harbour sediments. Environmental Toxicology and Chemistry, 22 (2003): 1535-1547.

Taborsky, B., **U. Dieckmann** and M. Heino (2003). Unexpected discontinuities in life-history evolution under size-dependent mortality. Proceedings of the Royal Society London Series B 270: 713–721.

Thiel, M., A. Zander, N. Valdivia, J.A. Baeza and **C. Rueffler**. Host fidelity of a symbiotic porcellanid crab: the importance of host characteristics. Journal of Zoology 261 (2003): 353-362.

Van Veller, M.G.P., D.R. Brooks, **M. Zandee**. Cladistic and Phylogenetic Biogeography: The Art and the Science of Discovery. Journal of Biogeography 30 (2003): 319-329.

Vinje, F., M. Heino, **U. Dieckmann**, O.R. Godø and J. Mork (2003). Spatial structure in length at age of cod in the Barents Sea. Journal of

Fish Biology 62: 549–564.

P.C. van Welzen, **H. Turner** and P. Hovenkamp. Historical biogeography of Southeast Asia and the West Pacific or the generality of unrooted area networks as historical biogeographic hypotheses. J. Biogeogr. 30 (2003): 181-192.

Wouters, A. Essay Review. Philosophers on Function. Acta Biotheoretica 51 (2003): 223-235.

Wouters, A.G. Four notions of biological function. Studies in History and Philosophy of Biological and Biomedical Sciences 34 (2003): 633-668.

Yokomizo, H., **P. Haccou** and Y. Iwasa. . Conservation Effort and Assessment of Population Size in Fluctuating Environments. Journal of Theoretical Biology 224 (2003): 167-182.

DISSERTATIONS

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